Multiple mechanisms underlie rapid expansion of an invasive alien plant

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Received: *24 October 2010*
Accepted: *3 March 2011*

New Phytologist (2011) **191**: 828–839
doi: 10.1111/j.1469-8137.2011.03720.x

Key words: *Ageratina adenophora*, Hengduan Mountains, multiple mechanisms, rapid invasion, Yangtze River.

Summary

- With growing concerns over serious ecological problems, a particular challenge is to reveal the complex mechanisms underlying rapid expansion of invasive species. *Ageratina adenophora* is of particular interest in addressing this question.
- We used geographic information systems and logistic regression to identify the geographic and environmental factors contributing to the presence of *A. adenophora*. Join-count spatial statistics with reproduction mode examination were employed to elucidate the spatiotemporal dispersal mechanisms.
- Multiple factors have significantly contributed to the rapid expansion of *A. adenophora*. Its biological traits, favoring dispersal by water and wind coupled with local spatiotemporally heterogeneous geography and ecology, promote invasion downstream and upstream along river valleys, while other factors associated with human activities facilitate its invasion over high mountains and across river valleys, providing new scope for progressive invasions. We further identified an unusual invasion event of *A. adenophora* subsequent to a great flood that amplified its dispersal ability from vegetative propagules and seeds.
- These findings suggest that dynamic interactions of multiple factors in heterogeneous ecogeographical environments – a 'combinatorial' invasion mechanism – would generate an unexpected invasion rate of an alien species or a seemingly stochastic invasion event.

Introduction

One of the critical determinants of spatial pattern and invasion rate is the dispersal mechanism of an invasive species and the way this interacts with abiotic and biotic variables in a new environment (Pysek & Hulme, 2005; Theoharides & Dukes, 2007). Knowledge of dispersal is essential to predict the ability of any species to track climate change and expand its range (Higgins *et al.*, 2001; Watkinson & Gill, 2002; Bullock *et al.*, 2006). Much work has concentrated on historical patterns of invasion and prediction of potential spread (Salo, 2005; Chauvel *et al.*, 2006; Wang & Wang, 2006; Lavoie *et al.*, 2007; Lelong *et al.*, 2007). However, the importance of the mechanism of dispersal is increasingly recognized as pest species cause ever more important problems (Pakeman, 2001; Nathan *et al.*, 2002; Tackenberg, 2003; Bullock *et al.*, 2006; Nathan, 2006; Truscott *et al.*, 2006; Theoharides & Dukes, 2007).

Some species, especially those undergoing unexpected rapid expansion, have the advantage of dispersal via more than one mechanism. *Mimulus guttatus*, for example, disperses by vegetative fragments and seeds depending on time of year, which promotes its rapid spread (Truscott *et al.*, 2006). Theoretically, different mechanisms of dispersal may result in diverse means of invasion that in combination with local geography and ecology may greatly promote spread (Mack, 2000; Drezner *et al.*, 2001; Soons *et al.*, 2004; Bullock *et al.*, 2006). However, studies of multiple dispersal mechanisms have received comparatively little attention. Nathan (2006) suggests that we need to consider dispersal by multiple vectors as the rule rather than the exception. Further, to understand the differences in spatial and temporal

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scales at which different mechanisms act, studies are needed that investigate mechanisms from explicitly observed data (Meng *et al.*, 2005) and to explore the linkage between mechanisms using a metamodeling approach (Wang *et al.*, 2008). Spatial models of invasion in natural systems are challenged by the integration of numerous spatiotemporal distribution data along with spatial variations in environmental factors, and a lack of historical data (Ristaino & Gumpertz, 2000; Kelly & Meentemeyer, 2002).

The biological features of an alien plant may influence its spread. The invasive perennial herb *Ageratina adenophora* is native to Mexico where it is common (Cronk & Fuller, 1995). Its asexual seeds are easily dispersed by wind and water because of their tiny size and ring of hairs. The plant can also spread by fragmented stems (Parsons & Cuthbertson, 2001). *Ageratina adenophora* first invaded the Yunnan province of China from Myanmar in the 1940s (Wang & Wang, 2006). Since then it has spread rapidly and caused serious damage to the local ecology and to agriculture (Wang & Wang, 2006). Our previous study (Wang & Wang, 2006) showed that range expansion of *A. adenophora* in Yunnan reached equilibrium in 1990. However, *A. adenophora* has not yet reached its potential distribution and is rapidly invading neighboring provinces, especially Sichuan and Chongqing in the eastern Hengduan Mountains and the upper reaches of the Yangtze River. Its average rate of expansion since 1990 has been 13.2 km yr^{-1} (Wang & Wang, 2006). This invasion rate is much higher than that of other alien plants in the area (Wang, 2006). We must, therefore, consider the possibility that its dispersal might involve diverse mechanisms.

Geographic and environmental features may influence the dispersal pattern of *A. adenophora*. The Hengduan Mountain range consists of very rugged terrain caused by the uplift of the Himalayas as a result of the collision of the Indian subcontinent with mainland Asia, *c.* 50 million years ago (Mya) (Sharma, 1984; Zhang *et al.*, 1997). This has created the peculiar, highly dissected topography of the Hengduan Mountains, in which high mountains alternate with deep gorges, aligned in parallel north to south (Wu, 1988; Zhang *et al.*, 1997). The topographic complex of these mountains correspondingly displays a wide range of microclimates, all of which are dominated by the Indian southwest monsoon and sometimes by the Pacific southeast monsoon, following seasonal changes in the wind system (Zhang *et al.*, 1997). The deeply dissected valleys and steep slopes were difficult for humans to reach, and this once protected the original forests and other ecosystems from disturbance. However, increasing population expansion and the rapid development of modern industry has resulted in railways and highways being constructed through these areas from the 1970s. Geographic and environmental conditions have thus been significantly changed, and the rapid expansion *A. adenophora* must be understood in this context.

In addition, with global warming and intensifying human disturbance of the ecology, extreme climatic events and ecological disasters are increasing in frequency (Jiang & Shi, 2003). The Yangtze River Valley provides a good example. An extensive flood occurred here in 1998 that appears to have facilitated long-distance dispersal of some invasive species, including *A. adenophora*.

Such a configuration of biological and environmental factors provides an opportunity to explore the potentially complex dispersal mechanisms of *A. adenophora*. Studies of dispersal are relatively difficult to carry out compared with studies of demography. Research progress is dependent on obtaining high-quality dispersal data (Skarpaas & Shea, 2007). As the ecological problems caused by *A. adenophora* are of great concern to local governments, agricultural departments and academic societies, a large quantity of detailed data are available from herbarium records and government documents, as well as our own long-term field investigations. We initially constructed spatial and temporal patterns of *A. adenophora* spread and then used logistic regression and join-count spatial statistics to identify operative mechanisms of dispersal that could have led to the pattern observed. Our aim was to explore potential multiple mechanisms responsible for the rapid invasion by *A. adenophora* of this unique and heterogeneous region. We focused on how the plant's diverse biological traits couple with the local environment and form an interplay that continuously promotes rapid invasion. Our research should encourage further exploration of possible mechanisms linking plant biology with spatial and temporal heterogeneity in the expansion of other invasive aliens.

Materials and Methods

Phytogeographic data

Historical distribution data for *A. adenophora* (Sprengel) R. King & H. Robinson (*Eupatorium adenophorum* Sprengel) (Asteraceae) in Sichuan, Chongqing and Hubei Provinces, were gained from Chinese central government and local government reports, herbarium specimens (see the Supporting Information, Notes S1) and published literature (Wang *et al.*, 1994; Zhou & Xie, 1999; Tao & Liu, 2002; Wang & Wang, 2006). To explore distribution more clearly, seven field investigations were carried out between 2001 and 2008 across the invaded region and adjacent areas (Notes S1). We investigated 200 sites, including 158 uninvaded sites and 42 occurrence points.

As in previous investigations, we used towns as basic spatial units to illustrate the expansion process. The earliest recorded invasion year in one town was defined as the invasion time. To illustrate spread more clearly and naturally, neighboring towns with same invasion time in a county were combined to form one locality. Thus, 153 localities were formed from 848

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towns in 44 invaded counties. Data on town boundaries were downloaded from the Data Sharing Infrastructure of Earth System Science (http://www.geodata.cn).

Data generated by geographical information systems and statistical analysis

We used geographical information systems (GIS) to map the invasion process. Expansion rates were estimated with ARCVIEW GIS software (ESRI Inc., Redlands, California, USA) by measuring linear distances between outmost occurrence points at a given time (e.g. 1978–1990, 1991–2000, 2001–2007), along upstream of the Anninghe River, G108 national road, Chengkun rail line and downstream of the Yalongjiang River and Jinshajiang-Yangtze River. Occurrence points in Zigui County, Hubei Province, are isolated and remote from the main invaded areas and were not used in calculating expansion rate. The GIS was used to calculate the number of occurrence points within 20, 15, 10 and 5 km of the rivers, road and rail line.

Using GIS and topographic maps (http://ngcc.sbsm.gov.cn/guide/), nine explanatory variables (V) were measured and associated with each locality. Maps were used to identify the direction (N, S, E, W, NE, NW, SE or SW; V1) within each locality to earliest invaded localities in Sichuan. It was hypothesized that N, NW and NE would receive more wind-dispersed seeds. The GIS was used to measure the minimum distance separating the central point of each locality from the Jinshajiang-Yangtze River (V2), Yalongjiang River (V3), Anninghe River (V4), Daduhe River (V5), G108 national road (V6), provincial road (V7) and Chengkun rail line (V8). We hypothesized that these rivers, roads and rail line might function as corridors of spread. We investigated whether the shorter the distance between a given location and a river, road or rail line with an *A. adenophora* population somewhere along it, the higher the probability of establishment of the plant at the given location. GIS was used to measure the altitude of the central point of each locality (V9); we hypothesized that higher elevation might be a natural barrier to establishment and spread.

Geographic and environmental factors that contributed to the presence of *A. adenophora* in different years were identified using binary logistic regression (Hosmer & Lemeshow, 2000; LeBlanc *et al.*, 2010). SPSS software (SPSS Inc., Chicago, Illinois, USA) was used for the calculations.

Join-count statistics as a measure of spatiotemporal diffusion

Spatial patterns of *A. adenophora* spread of provide clues to the process of its spread. The spatial process reflects interactions between the sites. The black and white (BW) join-count statistic is a simple way to measure the spatial association of data using different 'joins'. It is appropriate in our study to test hypothetical diffusion processes because of its ability to handle polygonal binary nominal data (Lee, 2003; Meng *et al.*, 2005). A BW join-count was used to measure the spatial autocorrelation of *A. adenophora* in Sichuan and Chongqing. If the locality reported an *A. adenophora* case, it was color-coded black (B), and if not, the locality was color-coded white (W). When two localities had some defined relationship such as a road link, they were considered to be linked by a 'join'. A join may link two B localities, two W localities or one B locality and one W locality; these were called BB, WW and BW joins, respectively. We counted the numbers of each type of join in Sichuan and Chongqing localities, and compared these with the expected number of each join under the null hypothesis, H_0, with no spatial autocorrelation among the localities. We found little difference between the results to aid selection of which of the three joint type statistics should be used as the indicator of autocorrelation. The BW statistics are used in this study. High negative values indicate clustering and high positive values indicate spacing. Details of the formulae for the BW test, its power and its interpretation are discussed at length by Cliff & Ord (1981) and Lee (2003).

Any join-count statistic will depend on the definition of a 'join'; a 'join' reflects a type of hypothetical interaction among spatial processes. We defined six joins to test geographical pattern development along wind direction, roads and rivers. As seeds of *A. adenophora* can be wind-dispersed, the wind spreading model (M-1) is based on the prevailing wind during the season of seed maturation. This model was designed to test spread by the prevailing southwest wind in the south-north oriented mountain valleys. Models 2, 3, 4, 5 and 6 are based on the river, road and rail systems, and were chosen because regression analysis showed that rivers, roads and rail lines may act as corridors of spread for *A. adenophora*. The road spreading model assumes that *A. adenophora* spreads in either direction along the G108 national road (M-2), and a similar model describes spread along the Chengkun rail line (M-3). The river spreading models including the Jinshajiang-Yangtze River spreading model (M-4), Anninghe River spreading model (M-5) and Yalongjiang River spreading model (M-6), assume that *A. adenophora* spreads in one direction along rivers, that is, downstream.

We calculated the *Z*-scores of the join count statistics for the six spreading models over time, and plotted the changes in *Z*-scores to determine a compact expansion, sprawling expansion or an in-filling expansion (Fig. 1). A detailed discussion of the temporal trends in *Z*-scores from join count statistics is provided by Lee (2003).

Reproduction and branching examination of earliest occurrences after 2000

Plant age was estimated by the branching structure of stems; this is highly correlated with life cycle (Yu, 2005). In

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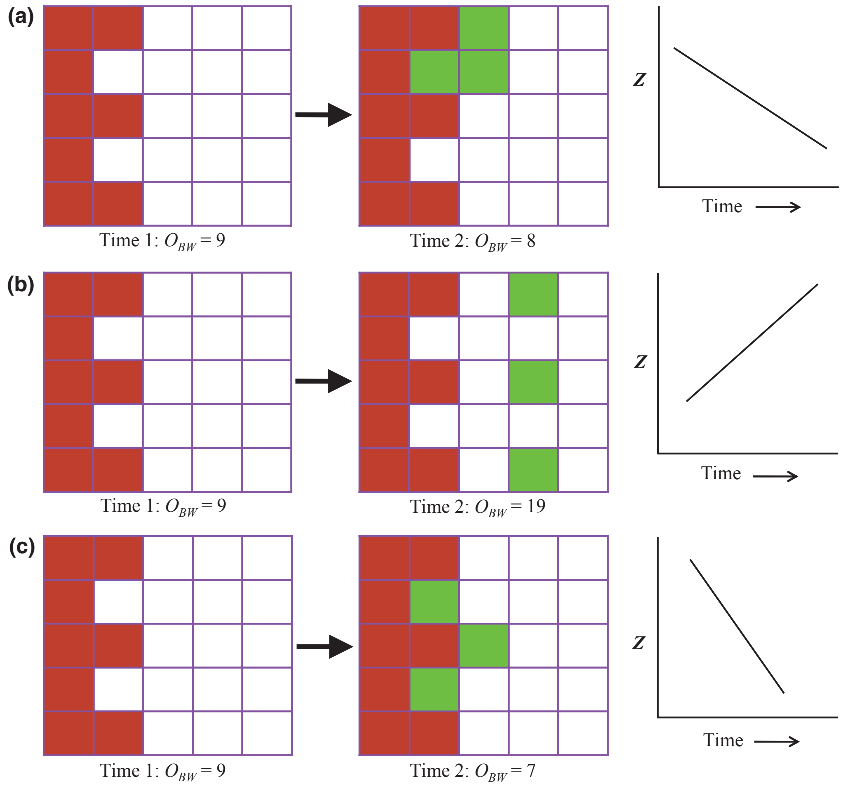

Fig. 1 Change in geographical patterns with new invasions of *Ageratina adenophora*, and three temporal trends in *Z*-scores from join-count statistics. (a) compact expansion, (b) sprawling expansion, (c) in-fill expansion. (Lee, 2003; reproduced with kind permission from Springer Science+Business Media B.V.).

Sichuan and Chongqing, the life cycle begins in May and June when seed germination takes place. Seedlings develop into adult plants within 12 weeks. The plant usually flowers the following March and produces many seeds. The apical bud withers at the end of the summer and growth is continued the following year by the lateral bud immediately below. Replication of this pattern results in a highly branched, sympodial structure; its age can thus be accurately calculated on the basis of this structure.

Ageratina adenophora can reproduce both by asexual seed and vegetatively by developing roots from stem nodes that are in contact with the soil surface. New shoots from lateral stem buds are able to grow into new plants. After several years the stem becomes a rudimentary rhizome. One can distinguish between seed-grown plants and vegetatively reproduced plants by investigating whether or not rudimentary stems are found in the root. We analysed reproduction mode and estimated the year of invasion for 42 earliest occurrences of the plant in the invaded localities after 2000 (Fig. 2).

Results

Invasion and spread of *Ageratina adenophora*

A total of 346 occurrences in 153 localities of 44 counties were used to reconstruct the historical invasion process of *A. adenophora* in Sichuan, Chongqing, and Hubei Provinces. This dynamic process is illustrated in our digital maps (Figs 2, 3) (see Notes S2 and Fig. S1 for the detailed invasion and spread process). The maps show that *A. adenophora* generally spread northeastwards along Jinshajiang-Yangtze River and northward along its tributaries and the road and rail line.

Expansion rates along the road and rivers in Sichuan and Chongqing varied during different periods (Fig. 4). Average expansion rates were 19 km yr^{-1} upstream along the Anninghe River and along the road and rail line to the north, and 33 km yr^{-1} downstream along the Yalongjiang and Jinshajiang-Yangtze rivers. However, an astounding 88 km yr^{-1} was attained along the Jinshajiang-Yangtze River after 2000.

Geographic distribution of occurrences

About 49% of the occurrence points were in areas within 5 km of rivers, the G108 road, and rail line. Approximately 23%, 15% and 5% of occurrence points were within 5–10 km, 10–15 km and 15–20 km from rivers, the G108 road and rail, respectively. In addition, our field investigations show that many occurrences along the Yangtze River after 2000 were at the confluences of tributaries with the Yangtze River, or in tortuous parts of the Yangtze River along the drift-line of the huge 1998 flood (Fig. S2).

Determinants of spatial diffusion

Of the nine explanatory variables tested by logistic regression, seven were significantly correlated with *A. adenophora*

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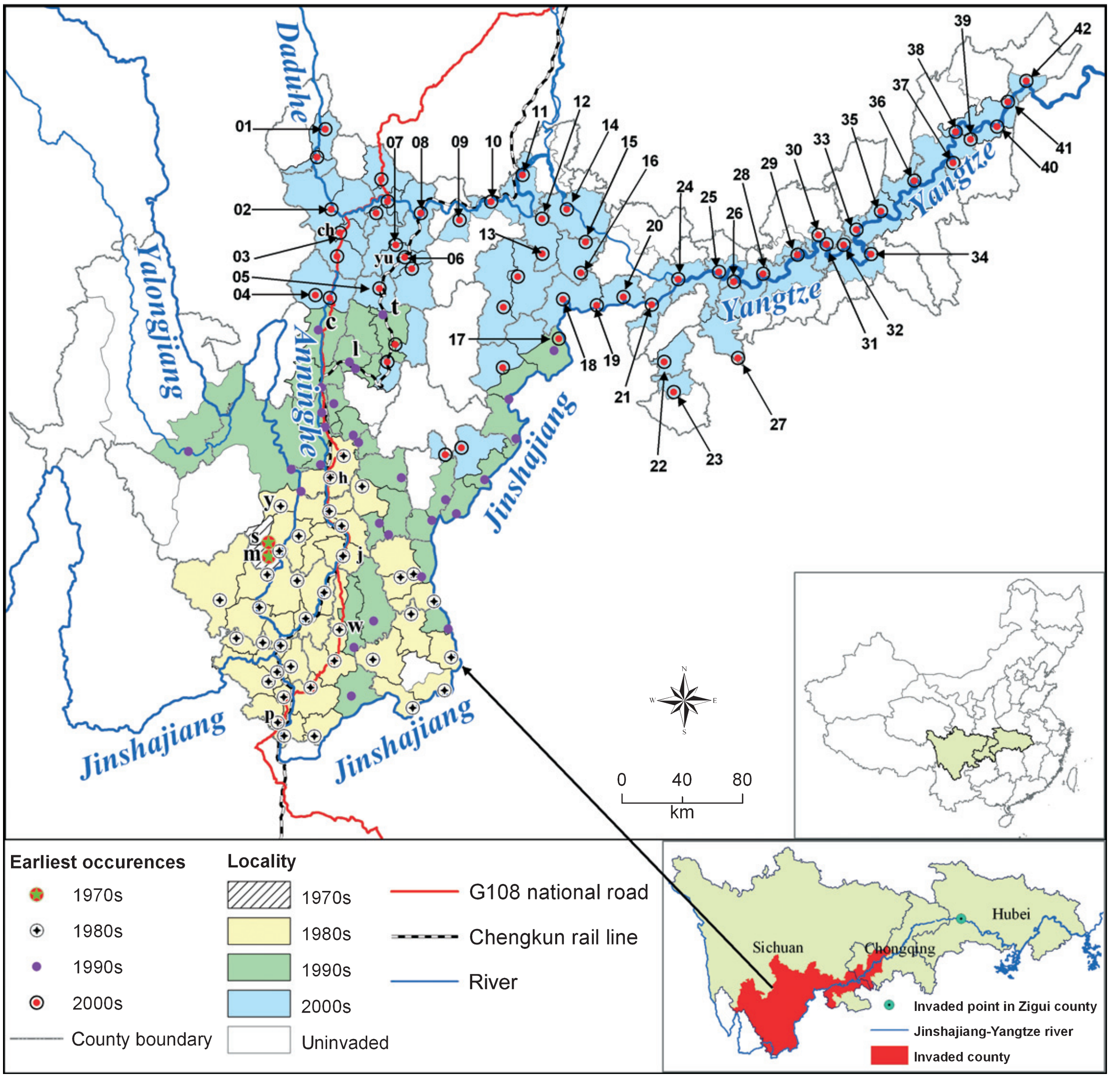

Fig. 2 Historical expansion of *Ageratina adenophora* in Sichuan, Chongqing, and Hubei Provinces. c, Chengxiang town; ch, Chaluo town; d, Dawan town; h, Huanglian town; j, Jinchuan town; l, Lake town; m, Malu town; p, Pingdi town; s, Shuhe town; t, Tiexi town; w, Waibei town; yu, Yutian town. The numbered arrows point to the earliest occurrences in the invaded localities after 2000 with the reproduction mode and invasion time examined.

distribution (the result of the analysis is listed in Table S1). The significant variables were different between years (Fig. 5). Significant variables explained 10.9–78.5% of the variance in their year of significance (Fig. 6). The negative regression coefficients indicated that the probability of finding a population of *A. adenophora* in a locality increased with proximity to the outlets of the Jinshajiang River, Anninghe River and the Jinshajiang-Yangtze River, and proximity to the G108 national road and Chengkun rail line (Fig. 5). This probability decreased with increasing the altitude (Fig. 5). A positive regression coefficient indicated that there is a higher probability of finding a population in the N, NW and NE of the earliest invaded localities in Sichuan than in the other directions (Fig. 5).

The overall results of the six spreading models calculated from join count statistics are shown in Fig. 7. The temporal trends of *Z*-scores for the six spreading models showed that the spatial distribution changed from sprawling to more compact over time, but expanded after 2000.

The road (M-2) and rail line (M-3) spreading models show that *A. adenophora* spread along the G108 road and rail line in a 'leap-frog' manner, with increasing *Z*-scores during the early phase of invasion (1978–1985) (Fig. 7). The occurrences are distributed separately along the G108 road and rail line in this period (Figs 2, 3). After 1986, newly invaded localities began to develop in a more localized manner with *Z*-values decreasing, until *A. adenophora* invaded the northern part of the Lingpai and Xiaoxiangling Mountains in 2003 and 2004 when *Z*-values were at their lowest (Figs 3, 7). After 2003 or 2004, newly invaded localities again began to spread out along the G108 road and Chengkun rail line (Figs 2, 3) and *Z*-scores increased again (Fig. 7).

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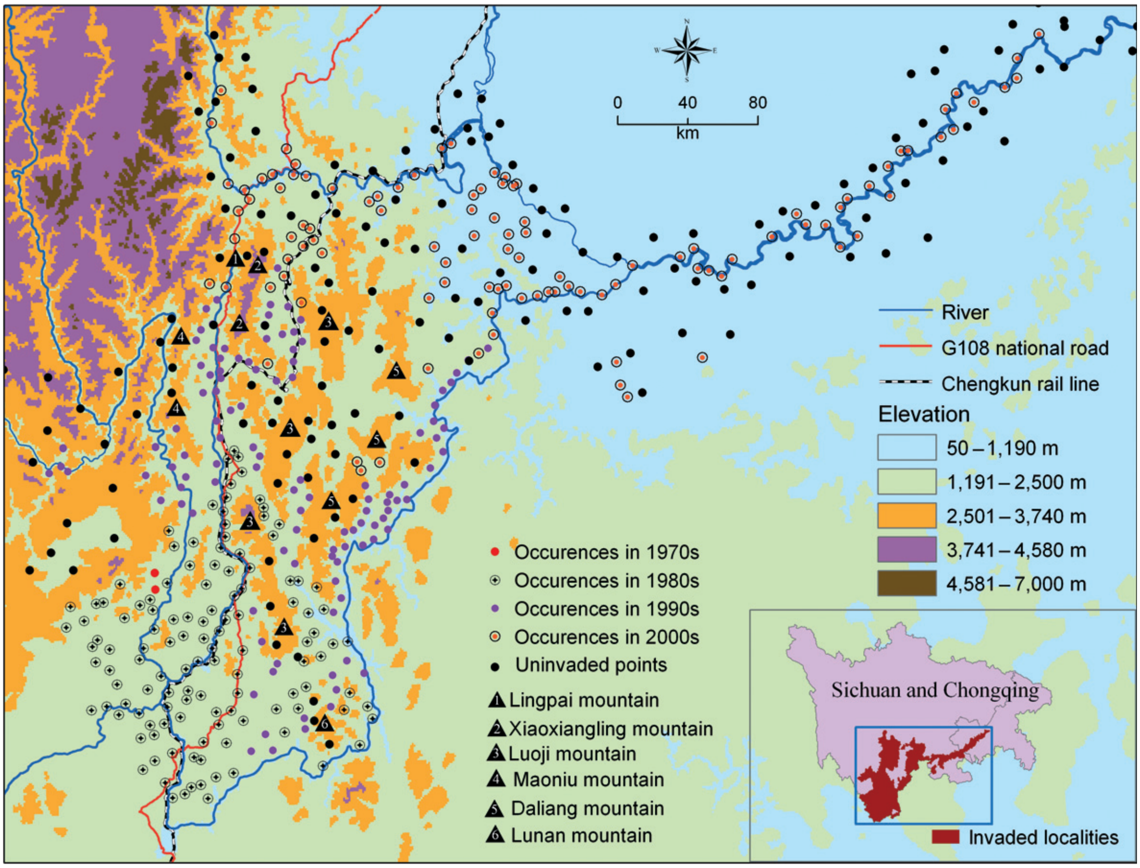

Fig. 3 Topographic map of distribution of *Ageratina adenophora* in Sichuan and Chongqing Provinces.

The temporal trends of the wind spreading model (M-1) and three river spreading models (M-4, 5 and 6) and the were almost identical to the road and rail line spreading models before 2000 (Fig. 7): thus the invaded locality along the rivers developed in the same manner as that along the road and rail line (Fig. 2). The sharp decrease of *Z*-scores for the Jinshajiang-Yangtze River spreading model (M-4) (Fig. 7), in particular, showed a sudden in-filling expansion process between 2000 and 2003.

Reproduction and branching examination of earliest occurrences after 2000

Among the 42 occurrences examined, most of those along the road and rail line are of seed-dispersed plants (Table S2). Occurrences along the Jinshajiang-Yangtze River were predominantly of vegetatively-dispersed plants; the estimated invasion here occurred in 1998 or 1999 (Table S2).

Discussion

Multiple models underlie the dynamic invasion pattern

Our spatial and temporal distribution statistics show that multiple processes have determined the spread of *A. adenophora* east of the Hengduan Mountains. Distribution patterns along the Yalongjiang River, Jinshajiang-Yangtze River, Anninghe River, G108 national road and Chengkun rail line vary between random, clustered, and dispersed (Fig. 7).

Observed distribution can result from many independent introductions spreading locally (stochastic), or from regional spread following introduction (Barney *et al.*, 2008). Invasive populations of *A. adenophora* appear to be randomly distributed in the early stages, becoming more clustered or dispersed as invasion proceeds (Fig. 7). Between 1978 and 1981, invasion developed in a random way in all models (Fig. 7). The plant first invaded Shuhe town(s) in Yanyuan County, then was recorded in the town of Pingdi (p), Panzhihua County (1980), and the town of Jinchuan (j), Dechang County (1981) (Figs 2, 3). Each of these isolated invasion points was the independent initial introduction of *A. adenophora* in Sichuan. Later, the invasion developed a rather different pattern. Over time, the distribution pattern of an invader may change from one form to another as new localities are invaded.

Between 1981 and 1985, *A. adenophora* was mainly distributed along the Jinshajiang-Yangtze River, Yalongjiang River, G108 national road and rail line (Figs 2, 3). The temporal trends of *Z*-values ($Z > +1.96$) imply that it spread

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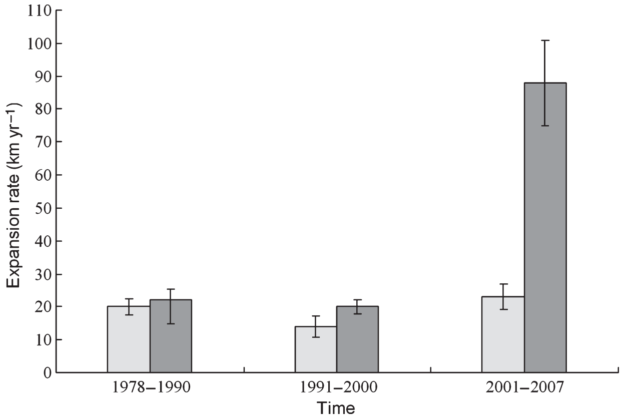

Fig. 4 Linear expansion rates of *Ageratina adenophora* during different periods along the road and rivers in Sichuan and Chongqing Provinces. Dark tinted bars, the expansion rate along the Yalongjiang, Jinshajiang-Yangtze River; light tinted bars, the expansion rate along the Anninghe River, G108 road and Chengkun rail line.

along the national road (G108), rail line and Yalongjiang River in a leap-frog manner during this period (Fig. 7). The newly invaded points were spaced apart as illustrated in Figs 2 and 3). This invasion pattern might be caused by long-distance dispersal of *A. adenophora* seeds with human activities along the road and rail line. Our field investigations support this hypothesis, as the plants along road and rail line were predominantly seed-grown.

The join count statistics demonstrate that the *Z*-scores for the Yalongjiang River, Anninghe River and Jinshajiang-Yangtze River spreading models between 1986 and 2000 are characterized by decreasing slopes. This indicates that spread during this period occurred in a compact or in-filling manner with newly invaded localities developing next to the invading localities (Fig. 1) (Lee, 2003). In this period, *A. adenophora* spread rapidly along the three river valleys as outlined earlier. As indicated by binary logistic regression analysis with a negative regression coefficient, populations of *A. adenophora* are more likely to occur within shorter distances from these rivers (Fig. 5). The dispersal of *A. adenophora* seed by water currents may have played a key role in downstream distribution during this period. In addition, the *Z*-scores for the wind spreading model are also characterized by a steeply decreasing slope between 1986 and 2000. Regression for this model shows that direction of invasion is significantly variable. Localities in the north and northwest of the primary invasion localities in Sichuan (i.e. upstream along the tributaries of the Jinshajiang-Yangtze River including the Yalongjiang and Anninghe Rivers), have higher probability of having a *A. adenophora* present (Fig. 5). Our field investigations show that during this period, in addition to dispersing downstream, the plant also rapidly spread upstream along the Yalongjiang and Anninghe Rivers aided, presumably, by the southwest wind dominant in this area. Wind-mediated dispersal of *A. adenophora* along the Anninghe River Valley can also explain its compact expansion along the national

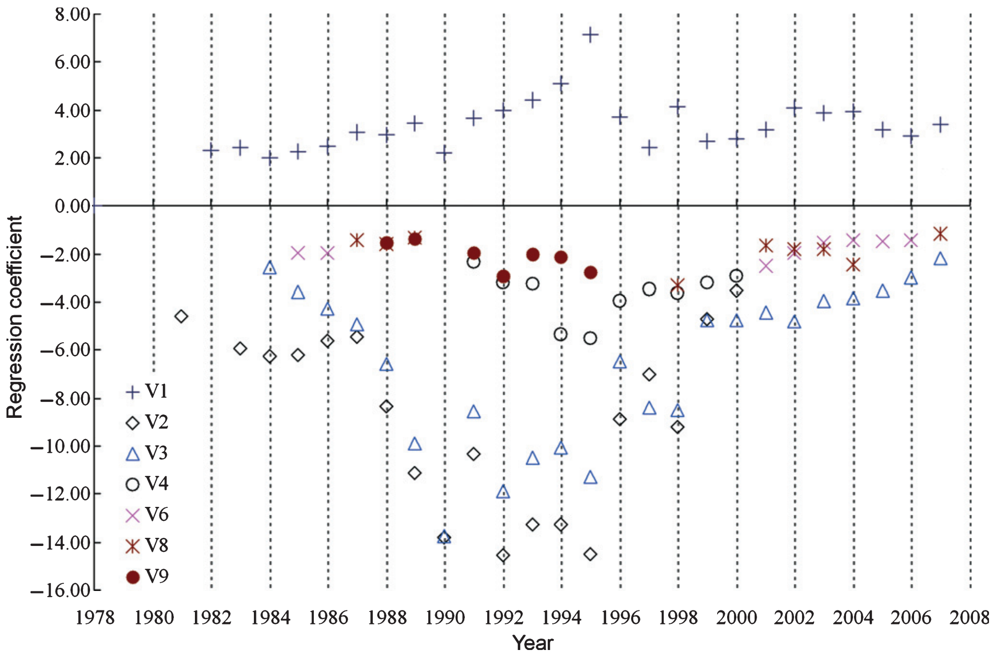

Fig. 5 Significant variables detected by binary logistic regression, and used to link an *Ageratina adenophora* population with chosen environmental variables. (V1) Direction (facing N, S, E, W, NE, NW, SE or SW); it was hypothesized that N, NW and NE would receive more wind-dispersed seeds. The minimum distance separating the central point of each locality from the Jinshajiang-Yangtze River (V2), Yalongjiang River (V3), Anninghe River (V4), G108 national road (V6), and Chengkun rail line (V8). V9, the elevation of the central point of each locality.

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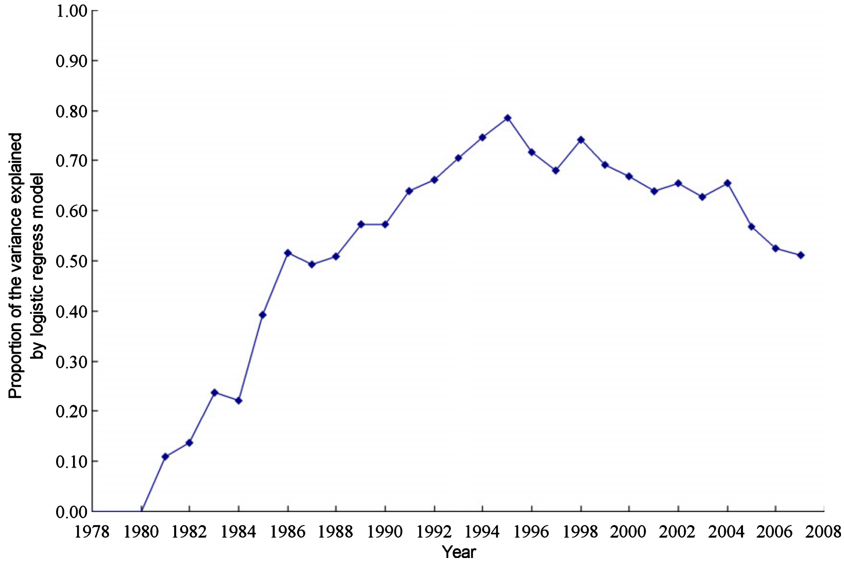

Fig. 6 Proportion of variance explained by the logistic model.

road and rail line between 1986 and 2003 because they lie along the river valleys before the G108 national road run across the Lingpai Mountain, as well as the Chengkun rail line run across the Xiaoxiangling Mountain (Fig. 3). After 2003, the *Z*-scores of the G108 national road and Chengkun rail line spreading models show increasing slope, indicating the sprawling manner of *A. adenophora* spread during that period. The join count statistics are strongly correlated with our field data, showing that *A. adenophora* further invaded and spread along the G108 national road and Chengkun rail line after crossing over the Lingpai and Xiaoxiangling Mountains (Fig. 3).

Interplay of multiple factors contributing to rapid spread of *A. adenophora*

The distribution pattern of any given species is a result of interaction between its biological characteristics and ecological conditions, over time (Burkart, 2001). An advantageous combination of abiotic and biotic variables encourages the spread of any given alien species. The historical and recent interplay between these factors determines invasion rate and distribution pattern. *Ageratina adenophora* reproduces by prolific asexual seed production; each individual produces 7000–10000 seeds that are very light, weighing *c.* 0.4 g per

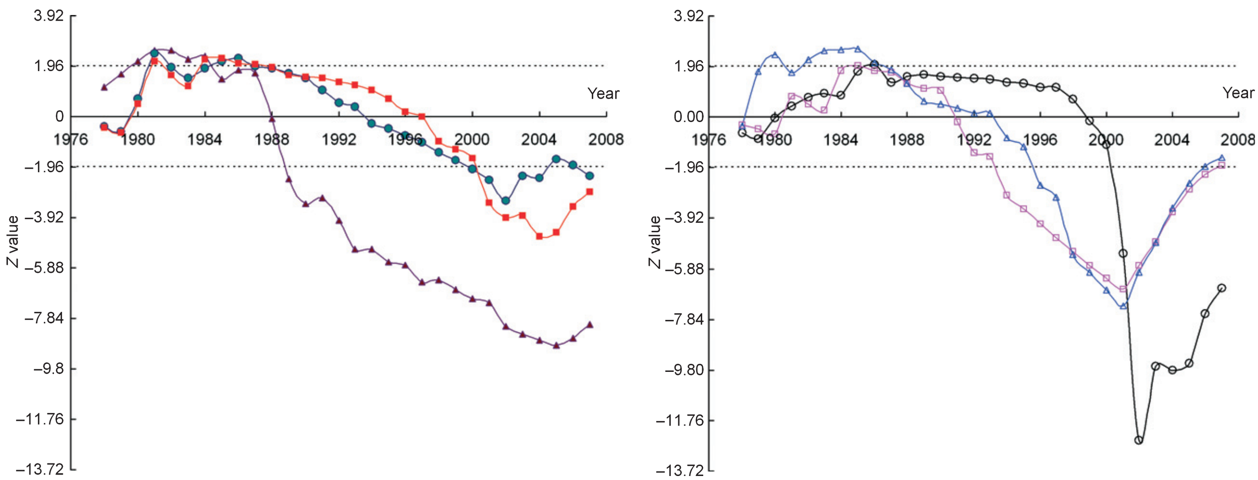

Fig. 7 Temporal trends in *Z*-scores from join-count statistics. Dashed line show positive and negative *Z*-score thresholds at *P* = 0.05. The range of *Z*-scores shows that the distribution pattern varies between random (*Z*–0), clustered (*Z* < 0) and dispersed (*Z* > 0). Solid line with closed triangle, wind spreading model (M-1), solid line with closed circle, G108 national road spreading model (M-2); solid line with closed square, Chengkun rail line spreading model (M-3); solid line with open circle, Jinshajiang-Yangtze river spreading model (M-4); solid line with open square, Anninghe river spreading model (M-5); solid line with open triangle, Yalongjiang river spreading model (M-6).

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1000 seeds (Auld & Martin, 1975; Liu *et al.*, 1985; Parsons & Cuthbertson, 2001). The tiny size and light weight of its seeds allows *A. adenophora* to be buoyant and dispersed by water over long distances. Evidence for downstream dispersal has previously been reported for the invasive *Fraxinus ornus* on the Herault River in southern France (Thebaud & Debussche, 1991). Taking into account the biological characteristics of *A. adenophora*, the *Z*-scores for different spreading models, and our field investigation, we believe that water dispersal of seeds (hydrochory) is the factor most responsible for its rapid expansion (33 km yr^{-1}) downstream along river valleys, and for the river corridor distribution patterns of this plant.

As hydrochory is only relevant to downstream spread, the invasion of *A. adenophora* upstream along river valleys and across high mountains is related to an interplay between other biological features and abiotic or biotic variables. In addition to its tiny size, the seed of this plant is also characterized by a specialized feather-like structure (pappus), attached to its seed coat. The pappus allows the seed to be readily dispersed by wind (Parsons & Cuthbertson, 2001). When seeds mature and are shed between March and April (Liu *et al.*, 1988), the southwestern monsoon is prevailing in southwest China, especially in the Hengduan Mountain area. As most river valleys in this region run in a north–south direction, the southwestern monsoon can easily disperse the seeds upstream along river valleys, including the Anninghe River and Yalongjiang River, and the tributaries of the Jinshajiang-Yangtze River. We believe that its compact spread upstream is predominantly facilitated by wind. This is demonstrated by the steeply decreasing *Z*-scores for the wind spreading model based on historical invasion dynamics between 1986 and 2003. The biological feature of the pappus, combined with the peculiar, parallel landscape features and the southwestern seasonal monsoon allow wind-dominated dispersal (Fig. 8).

Furthermore, the seeds of *A. adenophora* easily and frequently stick to clothing, footwear or passing vehicles and animals because of the pappus (Parsons & Cuthbertson, 2001; also the authors' observation). The tiny seeds can also spread as an impurity in sand and gravel used for road-making and in mud stuck to vehicles (Parsons & Cuthbertson, 2001; pers. comm. with Yong Liu, 2004). In addition, ecological disturbances including road construction, traffic, and maintenance activities frequently occur along roads and rail line, and these usually lie in or along river valleys. These human activities may remove some biological barriers, including competitors, and modify environmental characteristics in potential invasion sites (Parendes & Jones, 2000). The clearing of vegetation and soil during road construction and road-filling operations often creates bare areas and allows exotic plants to establish (Spellerberg, 1998; Trombulak & Frissell, 2000; Harrison *et al.*, 2002; Gelbard & Belnap, 2003; Lelong *et al.*, 2007). *Ageratina adenophora* is well adapted to colonize bare or intermittently bare areas

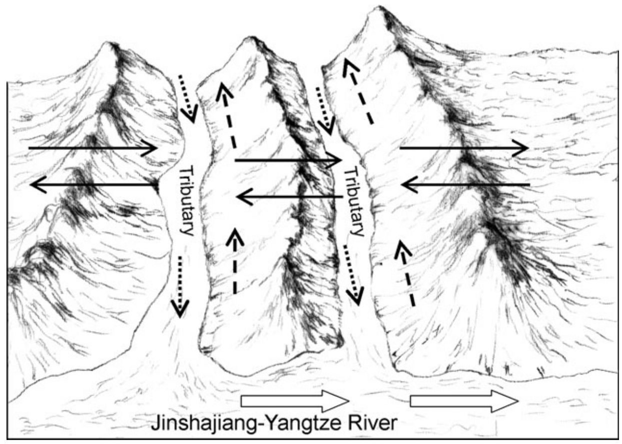

Fig. 8 Invasion and dispersal pathways and directions: interplay between biological traits and heterogeneous geography and ecology in the Hengduan Mountains and upper reaches of the Yangtze River. Note: Different types of arrows indicate differing invasion and dispersal pathways and directions along the Jinshajiang-Yangtze River and its tributaries. Dotted arrow, dispersal of seed or broken rhizome with the water current; dashed arrow, dispersal of seed along river valley upstream during southwest monsoon and via human activities; solid arrow, dispersal of seed by human activities; open arrow, dispersal of fragments of stems and rhizomes by the flood current during in the 1998 flood.

because it needs light for its seeds to germinate (Auld & Martin, 1975; Liu *et al.*, 1988). Consequently, such ecological disturbances along highway and railway lines probably accelerate the invasion process along river valleys. Thus, as indicated by the *Z*-scores for the G108 national road and Chengkun rail line spreading models, roads and rail line enhance spread, particularly upstream. In addition, roads and rail line with associated human activities might also be responsible for the invasion of adjacent streams reached over high mountains where the seed is unlikely to be wind-blown. The occurrence of *A. adenophora* along the rail line between the Xiaoxiangling and Luoji Mountains is a typical example of this kind of invasion, as well as the invaded sites along the G108 after 2000 in the Daduhe River Valley over the Lingpai Mountain (Fig. 3). Thus roads and rail line function as facilitators of invasion by overcoming natural physical barriers, especially high mountains (Fig. 8).

Unusual invasion event following the great flood

With water as its main vector, *A. adenophora* spread downstream along the Jinshajiang-Yangtze River at a rate of approximately 20 km yr^{-1} before 2000. However, the invasion rate increased dramatically along the Jinshajiang-Yangtze River after 2000 (to 88 km yr^{-1}). This dramatic rate is fourfold that before 2000 along this river. Previous studies have suggested that flooding might greatly facilitate the invasion process of alien plants along rivers by disturbing riparian vegetation (Fox & Fox, 1986; Kolliola & Puhakka,

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1988; Thebaud & Debussche, 1991; Pysek & Prach, 1993; Pyle, 1995; Truscott *et al.*, 2006). The 1998 flood along the Jinshajiang-Yangtze River was second only to the great flood of 1954; the latter was the largest of the 20th century in the Yangtze River area (Sun & Wang, 2002). The volume of the 1998 Jinshajiang-Yangtze River flood between the cities of Panzhihua and Chongqing was 1.78 times the mean flood volume for the 20th century (Sun & Wang, 2002). The incredible rate of spread of the plant after 2000 strongly correlates with the sharply decreasing slope of the *Z*-scores of Jinshajiang-Yangtze River spreading model between 2000 and 2003; these are perfectly coincident with the 1998 flood. In addition, after 2000, many new invasion points occurred at the confluences of the Yangtze and its tributaries. Occurrences were usually located along one bank of the tributary in the opposite direction to the flow of the Yangtze River, where water-carried debris easily accumulates (Fig. S2). The occurrences are along the drift line of the 1998 flood. According to Parsons & Cuthbertson (2001), *A. adenophora* also reproduces from the rhizome (rootstock) or through fragments of stems that touch the ground. Our field investigation also found that the newly invaded populations along the drift line of the 1998 Yangtze River flood were mainly from stem fragments functioning as rudimentary rhizomes. *Ageratina adenophora* had been widely and densely distributed around the Jinshajiang River Valley, from Panzhihua to Leibo County, in the upper reaches of the Yangtze, before 1998 (Figs 2, 3, S1). Field observations showed that individuals in the river valley suffered from mechanical damage following the flooding (e.g. partial uprooting or stem breakage). A strong river current can easily break stems above the ground and pull up rootstock because the plant is very shallow-rooted. A large number of stem fragments or broken rhizomes can be produced and propelled downstream with the flood. A destructive flood thus amplifies the vegetative dispersal ability of *A. adenophora.* Following the destruction or disturbance of other riparian vegetation, large openings are available and favorable for colonization (Walker *et al.*, 1986). We observed after 2000 that populations of *A. adenophora* were dense in riparian areas previously damaged by the Yangtze flood. Long-distance dispersal of a plant poses challenges for research because it involves rare events driven by complex and highly stochastic processes (Nathan, 2006). This unusual invasion event of *A. adenophora*, triggered by the second largest flood in 20th century China, is a prime example.

Conclusion

Many plant species are potentially dispersed by multiple processes. However, few studies properly address the full range of process and multiple vectors by which a species is dispersed (Bullock *et al.*, 2006). Our research demonstrates the utility of integrating field distribution data with GIS and spatial modeling; this approach allows us to map and understand the spread of exotic plants across large areas. One important contribution of our study is the finding that the rapid spread of *A. adenophora* in newly invaded regions is contingent upon the interaction of multiple factors, including the plant's biological traits and the local, spatiotemporally heterogeneous geography and ecology. This interplay of factors, biotic or abiotic and certain or uncertain, continuously promotes rapid invasion by water and wind. Frequent ecological disturbance caused by human activity along roads and rail line have facilitated invasion along river valleys and over mountains to adjacent valleys, in turn allowing natural dispersal to be repeated from new locations. In addition, the unusual event of a great flood amplified dispersal ability both from vegetative propagules and seeds. Unusually rapid expansion of invasive alien species frequently occurs against a background of ecological disturbance and global climate change. Our results provide new insight into methods of exploring multiple mechanisms that link spatial and temporal heterogeneity with diverse dispersal vectors. Complex combinatorial mechanisms may create an unexpected invasion rate or a seemingly stochastic rare invasion event. This understanding is crucial in developing appropriate and efficient strategies for preventing or minimizing invasion potential.

Acknowledgements

The authors are indebted to Dr Claude Lavoie and anonymous referees for valuable comments on this manuscript. The authors thank the following institutions and people for their help in field investigation and for providing invasion information: PE (Chinese National Herbarium, Institute of Botany, Chinese Academy Sciences); KUN (Herbarium of Kunming Institute of Botany, Chinese Academy Sciences); Wen-Long Gou, General Station on Grassland Husbandry of Sichuan province; Yong Liu, Liangshan District Grassland experiment Station; Jun-wei Ma, Animal Husbandry Bureau of Leshan city; Xiao-Jun Fu, Animal Husbandry Bureau of Muchuan county; Wen-Jin Li, Animal Husbandry Bureau of Leibo county; Hei-Ze Sha-Ma, Animal Husbandry Bureau of Zhaojue county; Wu-Niu A-Xi, Animal Husbandry Bureau of Meigu county; Jia-Yong Zhang, Animal Husbandry Bureau of Yibin city; Xiang-Hua Liu, Animal Husbandry Bureau of Jinyang county; Zai-Fu Chen, Animal Husbandry Bureau of Xide county; Feng Ma, Animal Husbandry Bureau of Butuo county; Animal Husbandry Bureau of Muli county; Xie Jie, Animal Husbandry Bureau of Qianwei county; Hua Li, Animal Husbandry Bureau of Pingshan county; Animal Husbandry Bureau of Ganluo county; Animal Husbandry Bureau of Shimian county. This research was supported by the National Basic Research and Development Program of China (973 Program 2009CB119200), and the National Nature Science Foundation of China (31000883).

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Supporting Information

Additional supporting information may be found in the online version of this article.

Fig. S1 Invasion dynamics of *Ageratina adenophora* in Sichuan, Chongqing, and Hubei Provinces.

Fig. S2 Distributional picture of *Ageratina adenophora* along the Yangtze river.

Table S1 Results of binary regression model that has been used to identify the geographic and environmental variables that contribute to the presence of *Ageratina adenophora* in different years

Table S2 Plant age estimated from branching systems of *Ageratina adenophora,* and reproduction method of selected plants

Notes S1 Field investigations, herbaria and reports examined.

Notes S2 Invasion and spread process of *Ageratina adenophora* in Sichuan, Chongqing and Hubei.

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